

Two new species of the *Phimochirus holthuisi* complex from the Gulf of Mexico, supported by morphology, color, and genetics (Crustacea: Anomura: Paguridae)

DARRYL L. FELDER^{1,3}, RAFAEL LEMAITRE² & CATHERINE CRAIG¹

¹Department of Biology and Laboratory for Crustacean Research, University of Louisiana at Lafayette, P.O. Box 42451, Lafayette, Louisiana 70504–2451, USA. E-mail: dlf4517@louisiana.edu

²Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, 4210 Silver Hill Road, Suitland, MD 20746, USA. E-mail: lemaitrr@si.edu

³Corresponding author

Abstract

Coloration, gene-sequence data (H3, 12s, 16s), and subtle features in morphology support the description of two new species, both formerly regarded to represent accepted variants of *Phimochirus holthuisi* s.l. While color in life consistently separates these species from *P. holthuisi* s.s. and from each other, morphological distinctions are subtle and less than absolute in small specimens, being based on ventral spine counts of walking leg dactyls and relative development of the superior crest on the major chela. Molecular phylogenetic analyses clearly support the separation of sister clades, representing two new species, from *P. holthuisi* s.s. as well as other congeners available for analysis. Both of the new species are presently known to occur widely throughout the northern Gulf of Mexico, though one occurs more commonly in the northeastern and southeastern Gulf, and may range as far south as Suriname. The other has been taken primarily in the northwestern Gulf, and is not known from outside Gulf waters. While both of the new species appear restricted to relatively deep subtidal waters of the continental shelf, *Phimochirus holthuisi* s.s. is instead more commonly found in shallow nearshore tropical waters on or near coral reefs. Previous literature reports of *P. holthuisi* usually represent, at least in part, one or both of these two new species.

Key words: Paguroidea, Paguridae, *Phimochirus*, new species, Gulf of Mexico

Introduction

The genus *Phimochirus* McLaughlin, 1981, with eight described species (five western Atlantic and three eastern Pacific), is one of 13 genera proposed to constitute the “*Pylopagurus-Tomopagurus*” group of hermit crab species by McLaughlin (1981a, b) and Lemaitre & McLaughlin (2003). Since those revisions, *Phimochirus holthuisi* (Provenzano, 1961) has been considered a morphologically highly variable species with a broad distribution in the western Atlantic from North Carolina and the Gulf Mexico throughout the Caribbean to Brazil (Felder *et al.* 2009). Yet, we have found that consistent differences in coloration of live specimens assignable to this presumed variable species occur in certain parts of its distributional range, despite a lack of obvious morphological differences. Owing to careful documentation of coloration in our recent collections, it has become very apparent that color patterns in our specimens from nearshore tropical reef habitats of Belize differ strikingly from those taken in deeper subtidal continental shelf habitats of the Gulf of Mexico. Furthermore, those from the Gulf of Mexico appear to themselves represent two distinct color variants.

As most of our photographic voucher specimens are of gene-sequence quality, we here undertake preliminary sequence comparisons of sampled populations assignable to *Phimochirus holthuisi* s.l., as well as to several available congeners, in order to clarify genetic relationships that might confirm species distinctions. Two new species, herein named, resolve as separate clades from the nominal species of this complex, conforming to separations based upon coloration differences. These are herein underpinned by detailed descriptive study, illustrations, and diagnostic comparisons of types and other museum specimens. To varied degrees, the majority of previous reports of *P. holthuisi* represent, in part, one or both of these two new species.

Materials and methods

Terminology herein departs from reference to fourteen cephalothoracic sternites, as used by some paguroid specialists (for example, McLaughlin 2003: fig. 2lm, n; Tudge *et al.* 2012: fig. 70.5G). While Forest *et al.* (2000) did not number the sternites of paguroids they studied, they did define them as ventral sternites of the “cephalothorax” rather than restricting them to the eight somites of the thorax (ie, thoracic sternites, excluding the cephalon), as is common practice of specialists working with many other groups of decapod crustaceans. To avoid confusion in the present paper, sternites are referred to only by the pereopod pairs between which they are ventrally positioned, thereby also identifying which of the posterior five thoracic somites they are derived from. Shield length (sl) was measured in millimeters (mm) to the nearest 0.1, from the tip of the rostrum to the posterior midpoint of the shield. Ovigerous females (ov) are indicated. Specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington DC (USNM), as part of the overall decapod collection of the University of Louisiana at Lafayette Zoological collections (ULLZ) that was recently transferred to the USNM. Among these are photographic and genetic vouchers as well as most other specimens used in this study that were originally referenced under ULLZ catalog numbers, which are herein indicated along with their newly issued corresponding USNM numbers. All had been directly preserved in 80% ethyl alcohol (EtOH) or first frozen in seawater or glycerol at -80°C before later transfer to 80% EtOH. Additional specimens were sequenced from holdings of the Florida Museum of Natural History, University of Florida, Gainesville (UF).

Line illustrations were made on a Wild M5 dissecting microscope with a camera lucida. Where required, chlorazole black staining was used to enhance contrast of morphological features. Photographs were assembled from a combination of digital exposures taken with a 60 mm Nikkor macrolens under 5000°K artificial illumination and digital scans of Kodachrome 25 color slide images taken with a 55 mm Nikkor lens in direct and reflected natural sunlight. At sea, clove oil or a salt/ice bath was used to immobilize specimens prior to photography. Alternatively, some specimens were briefly frozen in seawater and defrosted immediately prior to photography. In both cases, specimens were positioned below the water surface in a shallow water-filled tray with the bottom lined by black felt.

Genomic DNA was extracted from gills, abdominal tissues, eggs, or whole appendages of selected sequence-quality specimens (Table 1), using the Qiagen DNeasy DNA extraction kit (Qiagen, Cat. No. 69504). DNA purity and concentration was evaluated using the NanoDrop Lite Spectrophotometer (ThermoFisher Scientific, Cat. No. ND-LITE-PR). Partial sequences of H3 nuclear DNA, 12s mtDNA, and 16s mtDNA were amplified using primers and temperature profiles in Table 2. Reactions applied established protocols (Thoma *et al.* 2014) with primer concentrations varying from 0.2 μ M to 0.8 μ M; 1 μ L 1% Bovine Serum Albumin (BSA) substituted for Betaine in some reactions. PCR products were purified using SureClean Plus (Bioline USA Inc, SKU 37047). Cycle sequencing reactions and clean-up followed Thoma *et al.* (2014) with the protocol for cycle sequencing modified to accommodate the use of BDX64 Big-Dye Enhancing Buffer (Molecular Cloning Labs, Cat. No. BDX-100) for some samples. Sequence contigs were trimmed and assembled in Sequencher version 4.1.2 (GeneCodes Corporation, Ann Arbor, MI). A multiple sequence alignment was generated for each marker individually in MAFFT under G-INS-i criteria for H3, and E-INS-i criteria for 12s and 16s (Katoh *et al.* 2017). Ambiguously aligned regions were trimmed from each alignment with GBLOCKS (Castresana 2000), using default parameters for the H3 marker and the following modifications for the 12s and 16s alignments: 1) minimum length of block = 8; 2) allowed gap positions = half. Resulting single-gene alignments were concatenated into a single aligned matrix in BioEdit (Hall 1999). Model partitions were assigned for each of the three individual markers, with the H3 marker further partitioned by codon position. A Maximum Likelihood (ML) phylogeny with 1000 bootstrap replicates was inferred using the RAxML (Stamatakis 2006) Black-Box tool available on the CIPRES Science Gateway (Miller *et al.* 2010) with the GTR +Gamma model of nucleotide substitution applied to each partition (Rodriguez *et al.* 1990). A companion Bayesian analysis was run in MrBayes version 3.2.6 (Ronquist *et al.* 2012). A 4-chain Markov Chain Monte Carlo (MCMC) algorithm with heated chains at a temperature of 0.5 ran for 4,000,000 generations, sampling one tree every 1,000 generations. Run parameters were observed in TRACER version 1.7.1 (Rambaut *et al.* 2018) to confirm analysis convergence; it was calculated that 500,000 trees (12.5%) should be discarded as burn-in. A 50% majority rule consensus tree was derived from the remaining trees in Mesquite version 3.4 (Maddison & Maddison 2017). Bayesian posterior probabilities calculated for the consensus tree were used to evaluate confidence in congruent clades in both the ML and Bayesian results.

TABLE 1. Paguroid species used for ML and Bayesian phylogenetic inferences, showing catalog number, collection locality, and NCBI GenBank accession numbers for partial sequences of H3, 12s mtDNA, and 16s mtDNA. Dashes (“–”) denote unavailable sequence data. (Museum abbreviations: ULLZ = University of Louisiana at Lafayette Zoological Collection, Lafayette, Louisiana; USNM = National Museum of Natural History, Smithsonian Institution, Washington D.C.; UF = Florida Museum of Natural History Invertebrate Zoology Collection, University of Florida, Gainesville, Florida.)

Family	Taxon Name	Museum catalog No.	Country: Locality	Accession Number H3 / 12s / 16s
Paguridae				
	<i>Phimochirus</i> cf. <i>holthuisi</i>	ULLZ 7685 / USNM 1543129	USA: Florida, northeastern Gulf of Mexico	MK830050 / – / MK848221
	<i>Phimochirus</i> cf. <i>holthuisi</i>	ULLZ 7847 / USNM 1543313	USA: Florida, northeastern Gulf of Mexico	– / MK848203 / –
	<i>Phimochirus</i> cf. <i>holthuisi</i>	ULLZ 14352 / USNM 1547566	USA: Florida, northeastern Gulf of Mexico	MK830053 / MK848204 / MK848222
	<i>Phimochirus</i> cf. <i>holthuisi</i>	ULLZ 14572 / USNM 1547705	USA: Louisiana, northwestern Gulf of Mexico	MK830048 / MK848205 / MK848223
	<i>Phimochirus</i> cf. <i>holthuisi</i>	ULLZ 5789 / USNM 1541146	USA: Louisiana, northern Gulf of Mexico	MK830051 / MK848206 / MK848224
	<i>Phimochirus</i> cf. <i>holthuisi</i>	ULLZ 5814 / USNM 1541669	USA: southeastern Gulf of Mexico	MK830049 / MK848207 / –
	<i>Phimochirus</i> cf. <i>holthuisi</i>	ULLZ 7825 / USNM 1543233	USA: northwestern Gulf of Mexico	MK830052 / MK848208 / MK848225
	<i>Phimochirus</i> cf. <i>holthuisi</i>	ULLZ 7973 / USNM 1543319	USA: Florida, northeastern Gulf of Mexico	KF182678 / KF182415 / KF182578
	<i>Phimochirus</i> cf. <i>holthuisi</i>	ULLZ 13837 / USNM 1547302	USA: Louisiana, northern Gulf of Mexico	– / MK848209 / MK848226
	<i>Phimochirus holthuisi</i> s.s.	ULLZ 16588 / USNM 1558313	Belize: Carrie Bow Cay, Caribbean Sea	MK830047 / MK848210 / MK848227
	<i>Phimochirus operculatus</i>	UF 026018	USA: Florida, eastern Gulf of Mexico	– / MK848211 / MK848228
	<i>Phimochirus operculatus</i>	ULLZ 9917 / USNM 1534602	Belize: Carrie Bow Cay, Caribbean	MK830046 / MK848212 / MK848229
	<i>Phimochirus randalli</i>	ULLZ 7345 / USNM 1541699	Mexico: Yucatan Peninsula, southern Gulf of Mexico	KF182677 / KF182418 / KF182577
	<i>Phimochirus randalli</i>	ULLZ 7071 / USNM 1541890	Mexico: Yucatan Peninsula, southern Gulf of Mexico	KF182676 / KF182417 / KF182576
	<i>Phimochirus</i> sp.	ULLZ 9677 / USNM 1544505	Panama: Pacific Ocean	MK830045 / MK848214 / MK848230
	<i>Phimochirus</i> sp.	ULLZ 9679 / USNM 1544507	Panama: Pacific Ocean	– / MK848213 / –
Outgroup				
Paguridae				
	<i>Agaricochirus</i> sp.	USNM 1297342	Curaçao: southern Caribbean Sea	MK830040 / MK848215 / MK848231
	<i>Goreopagurus piercei</i>	ULLZ 14582 / USNM 1547712	USA: Texas, northwestern Gulf of Mexico	MK830043 / MK848216 / MK848232
	<i>Manucomplanus unguulatus</i>	ULLZ 14401 / USNM 1547537	USA: Florida, eastern Gulf of Mexico	MK830039 / MK848217 / MK848233

....Continued next page

TABLE 1. (Continued)

Family	Taxon Name	Museum catalog No.	Country: Locality	Accession Number H3 / 12s / 16s
	<i>Pagurus bullisi</i>	ULLZ 14475 / USNM 1547757	USA: Louisiana, northern Gulf of Mexico	MK830042 / MK848218 / MK848234
	<i>Pylopagurus discoidalis</i>	ULLZ 14483 / USNM 1547761	Lesser Antilles: Saba Bank, Caribbean Sea	MK830041 / MK848219 / MK848235
	<i>Rhodochirus rosaceus</i>	ULLZ 13830 / USNM 1547296	USA: northern Gulf of Mexico	MK830044 / MK848220 / MK848236

TABLE 2. Primers and corresponding Polymerase Chain Reaction temperature profiles used in this study. References for each primer set indicated in last column.

Gene	Primer	Primer Sequence	Annealing Temperatures	Reference
Histone 3	forward: H3af	5' - ATGGCTCTGACCAAGCAGACVGC - 3'	50–54°C for 30–60 seconds	Colgan <i>et al.</i> (1998)
Histone 3	reverse: H3r	5' - ATATCCTTRGGCATRGTGAC - 3'		Colgan <i>et al.</i> (1998)
12s mtDNA	forward: 12sf	5' - GAAACCAGGATTAGATACCC - 3'	50–54°C for 30–60 seconds	Buhay <i>et al.</i> (2007)
12s mtDNA	reverse: 12s1r	5' - AGCGACGGGCGATATGTATAG - 3'		Buhay <i>et al.</i> (2007)
16s mtDNA	forward: 16s 1472	5' - AGATAGAAACCAACCTGG - 3'	50–54°C for 30–60 seconds	Crandall & Fitzpatrick (1996)
16s mtDNA	reverse: 16sL2	5' - TGCCTGTTTATCAAAAACAT - 3'		Schubart <i>et al.</i> (2002)
16s mtDNA	reverse: 16sar	5' - CGCCTGTTTATCAAAAACAT - 3'		Palumbi <i>et al.</i> (1991)
16s mtDNA	forward: 16s- CWC-01f	5' - TAAAGTCTAGCCTGCCCACT - 3'		new
16s mtDNA	reverse: 16s- CWC-01r	5' - CCGGTTTGAACCTCAAATCATGT - 3'		new

Molecular phylogenetic inferences

A concatenated analysis based upon sequences of the H3 nuclear, 12s mitochondrial, and 16s mitochondrial genes yielded a Maximum Likelihood (ML) phylogenetic tree with highly supported definition of three clades that have all, to date, been assignable to *Phimochirus holthuisi* s.l. on the basis of long-accepted morphological characters (Fig. 1). One among these, hereafter regarded as *P. holthuisi* s.s., closely matches the color description furnished by Provenzano (1961), herein represented by specimens depicted in Fig. 2A, B. Two others (*Phimochirus* cf. *holthuisi*, clades “I” and “II”) differ from it strikingly in color, and are named as new species in the taxonomic treatment that follows. All three are well separated from clades defining other described and undescribed congeners that were available for inclusion in the analyses. Among those are two western Atlantic sympatric species of similar size and habitat, *Phimochirus operculatus* and *Phimochirus randalli*. While the somewhat smaller sized but also regionally distributed *Phimochirus leurocarpus* McLaughlin, 1981 may at least slightly overlap ranges of the two new species, especially in the extreme eastern Gulf of Mexico, sequence quality specimens of this species were not available for inclusion in analyses. However, *P. leurocarpus* differs conspicuously from members of the *Phimochirus holthuisi* complex in color and morphology (McLaughlin 1981b). Taxonomic treatments of two represented Pacific populations are reserved for future studies.

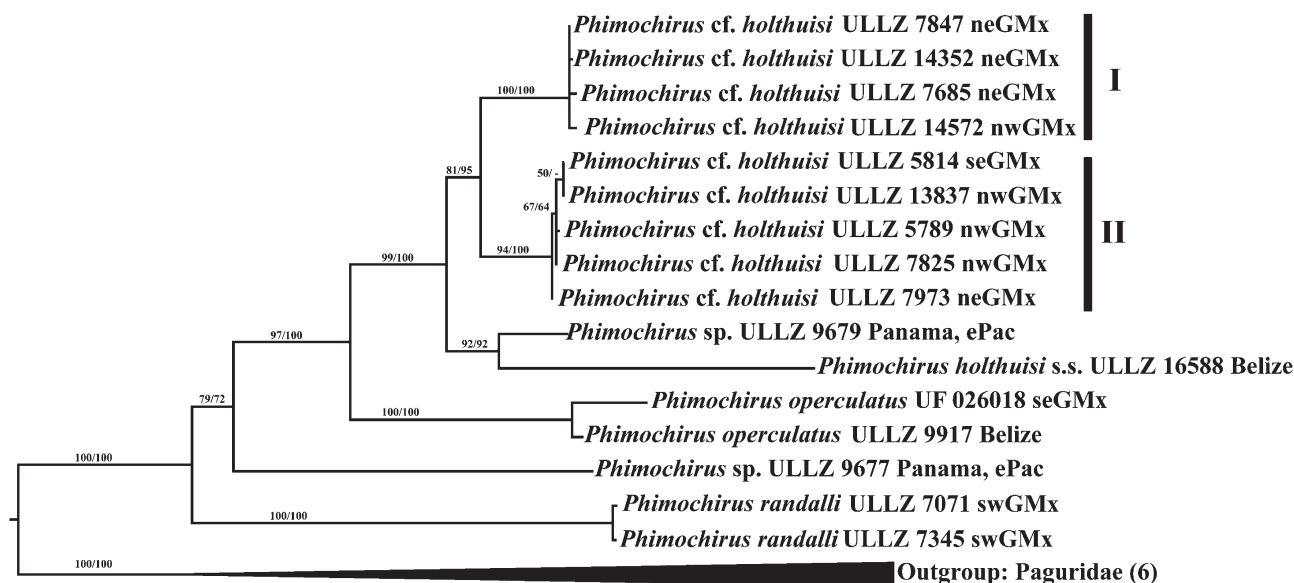


FIGURE 1. Maximum Likelihood phylogeny inferred in RAxML based on H3 nuclear DNA, 12s mtDNA, and 16s mtDNA. Bootstrap support values (bs) and Bayesian posterior probabilities (bp) with values greater than 50 are displayed above branches at tree nodes with the notation bs/bp. Clades I and II, assigned a priori to *Phimochirus cf. holthuisi*, are delimited by vertical black bars and correspond to two new species herein described. For branch labels, taxon name is followed by voucher catalog number (see Table 1) and collection locality. Abbreviations: eGMx = eastern Gulf of Mexico, ePac = eastern Pacific, neGMx = northeastern Gulf of Mexico, nwGMx = northwestern Gulf of Mexico, seGMx = southeastern Gulf of Mexico, swGMx = southwestern Gulf of Mexico.

Taxonomy

Family Paguridae

Phimochirus holthuisi (Provenzano, 1961) s.s.

(Figs 1; 2A, B; 3; 4; Tab. 1)

Pylopagurus operculatus.—Holthuis, 1959: 157 (in part?), not fig. 31 (= *Phimochirus formani* **nov. sp.**); Hazlett, 1966: 86; Rodríguez, 1980: 234. [See Remarks].

Pylopagurus holthuisi Provenzano, 1961: 162, fig. 3 (type locality: 4.5 miles Southeast of Ram's Head, St. John, U.S. Virgin Islands, 15–18 m) (in part); Felder, 1973: 30, fig. 13 (in part). [See Remarks].

?*Pylopagurus holthuisi*.—Coelho & Ramos, 1973: 165; Coelho & Santos, 1980: 143; Coelho & Ramos-Porto, 1986: 42.

Pylopagurus samariensis Sánchez, 1978: 215, figs 1–5; Sánchez & Campos, 1978: 58, fig. 22.

Phimochirus holthuisi.—McLaughlin, 1981a: 5; McLaughlin, 1981b: 342, figs 4c, 6a–c, 7c (in part); Williams, 1984: 225 (in part), not fig. 161 (= *Phimochirus formani* **nov. sp.**); Abele & Kim, 1986: 34, 383 unnumbered fig. c, d (in part); Lemaitre & McLaughlin, 2003: 466, tab. 1 (in part); Mejía-Ortiz *et al.*, 2008: 232; Felder *et al.*, 2009: 1071 (in part); McLaughlin *et al.*, 2010: 34. [See Remarks]; Martínez-Campos *et al.*, 2017: 292 (unnumbered figs a–c), 293, figs 4.75, 6.35 [see Remarks]; Poupin, 2018: 166, fig. 170.

?*Phimochirus holthuisi*.—Gore & Scotto, 1983: 93, figs 1–6 [larvae]; Hernández-Aguilera *et al.* 1996: 49; Rieger, 1998: 421; Melo, 1999: 140, figs 81, 82; Martínez-Campos *et al.*, 2012: 248, tab. 4; Rodríguez-Almaraz *et al.*, 2005: 322, not fig. 40 (= *Phimochirus formani* **nov. sp.**); Wicksten, 2005: 32, tab. 1; Coelho *et al.*, 2007: 10, tab. 4; Nucci & Melo, 2011: 36, figs 1J, 2J, 3J; Lemaitre & Tavares, 2015: 454, tab. 1. [See Remarks].

Type material. Holotype: male, sl 4.2 mm (USNM 107155), 4.5 miles Southeast of Ram's Head, St. John, U. S. Virgin Islands, sand patch on coral rock bottom, 15–18 m, 3 Feb 1961.

Additional material. *Southeastern United States.* 1 ov female, sl 2.7 mm (USNM 191093), 91 m, Cape Look-out, North Carolina, Oct 1963; 1 ov female, sl 2.4 mm (USNM 191094) 24° 54' N, 75° 32' W, 51 m, off North Carolina, R/V Silver Bay, sta 2926, 23 Mar 1967; 3 males, sl 1.6–2.2 mm, 1 female, sl 2.1 mm, 2 damaged specimens (USNM 150224), 31° 26.53' N, 79° 42.22' W, 252–291 m, off Sapelo Island, Georgia, 6 Aug 1963. *Caribbean Sea.*

1 male, sl 3.7 mm (USNM 1111037) Jamaica, Drax Cove, St. Ann's Bay, intertidal/shallow water, 14 May 2005; 1 male, sl 3.3 mm (USNM 1542650 = ULLZ 3564), patch reef behind crest, 2.0 m, Carrie Bow Cay, Belize, 27 Apr 1983; male, 3.3 mm (USNM 1558313 = ULLZ 16588), rubble atop spur on reef front, 4.0 m, Carrie Bow Cay, Belize, 28 Apr 2015.



FIGURE 2. *Phimochirus holthuisi* (Provenzano, 1961) s.s.: A, male, sl 3.3 mm (USNM 1542650 = ULLZ 3564), Belize; B, male, sl 2.9 mm (USNM 1558313 = ULLZ 16588), Belize. *Phimochirus formani* **nov. sp.**: C, male paratype, sl 3.1 mm (USNM 1547566 = ULLZ 14352), northeastern Gulf of Mexico; D, male paratype, sl 2.8 mm (USNM 1543170 = ULLZ 7711), north-eastern Gulf of Mexico. *Phimochirus tunnelli* **nov. sp.**: E, male paratype, sl 4.1 mm (USNM 1545269 = ULLZ 10611), north-western Gulf of Mexico; F, ov female paratype, sl 3.9 mm (USNM 1541146 = ULLZ 5789), northwestern Gulf of Mexico.

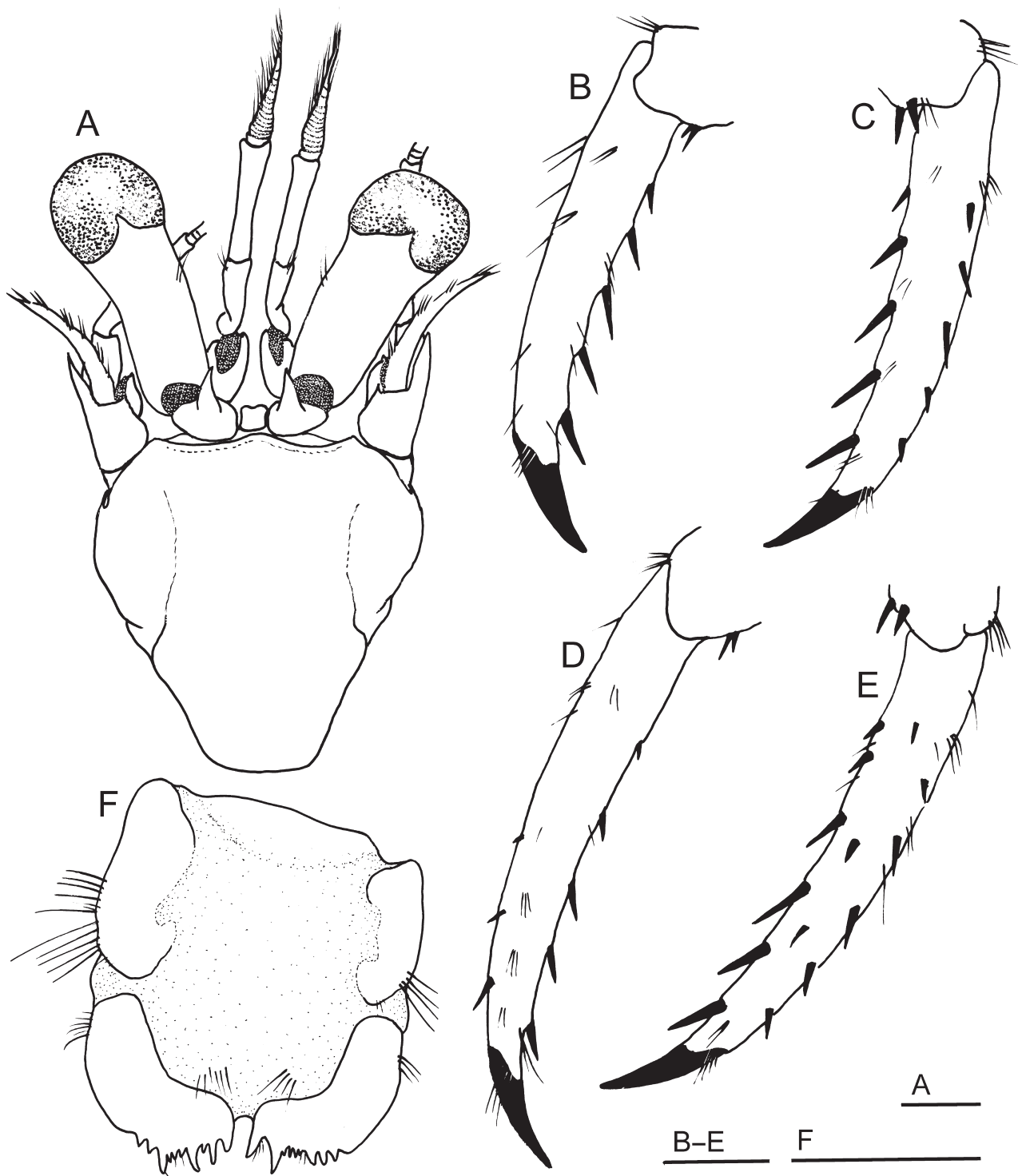


FIGURE 3. *Phimochirus holthuisi* (Provenzano, 1961) male holotype, sl 4.2 mm (USNM 10515), U. S. Virgin Islands. A, cephalothorax, eyes, and frontal appendages, dorsal surface; B, left second pereopod dactyl, lateral surface; C, left second pereopod dactyl, mesial surface; D, left third pereopod dactyl, lateral surface; E, left third pereopod dactyl, mesial surface; F, telson, dorsal surface. Scale bars = 1.0 mm.

Diagnosis. Carapace shield approximately as long as broad; rostrum broadly subtriangular, rounded. Antennular and antennal peduncles at most reaching to distal margin of corneas; antennal flagella with short setae 1 or less flagellar article in length. Right chela with dorsal surface of fixed finger with small, low nearly obsolete tubercles; palm with dorsal surface smooth, lateral and mesial margins sharply defined by weakly crenulate ridge, mesial margin expanded distally and terminating in strong, blunt spiniform angle. Carpus with dorsomesial margin weakly

defined by low ridge armed with 1 proximal spine and 2 or 3 small, blunt spines distally. Dactyls of second and third pereopods approximately 1.7 times longer than propodi; dorsomesial margins each with usually 5 corneous spinules, ventromesial margins each with row of usually 5 or 6 corneous spinules. Anterior lobe of sternite between third pereopods subsemiovate, with simple setae; sternite between fourth and fifth pereopods with simple setae. GenBank sequence accession numbers for Belize specimen (USNM 1558313 = ULLZ 16588): (H3) MK830047; (12s) MK848210; (16s) 848227.

Color. In life (Fig. 2A, B), body overall color whitish to pale yellow-brown to rust, with primary patterning of narrow brown lines, carapace overall marked by dark narrow broken longitudinal lines of brown on whitish background; major chela almost entirely white to off white; ocular peduncle with narrow band of brown proximally.

Habitat. Occupying variety of medium sized gastropod shells, including faciolariids, turbinids, and muricids; coral reefs, on coralline sand and rubble substrates of spur and groove reef front to backreef lagoon rubble, sands, and seagrass beds; reef crests and shallow adjacent subtidal waters; inner continental shelf; most commonly 2–18 m, to 91 m off North Carolina, perhaps to 291 m off Georgia.

Distribution. Western Atlantic: East coast of the United States, off North Carolina and Georgia; Caribbean, including Quintana Roo (Cozumel), Belize, Virgin Islands, Jamaica, Guadeloupe, and Colombia; questionably north-eastern coast of South America, Suriname to Brazil.

Remarks. The study of numerous specimens considered to be members of the *Phimochirus holthuisi* complex has shown that, in addition to coloration, a number of subtle yet diagnostic characters can be used to redefine and restrict Provenzano's (1961) taxon. In the absence of coloration, *P. holthuisi* s.s. can be differentiated, with caution, from the two new congeneric species described herein by several reliable, albeit subtle, characters that include the shape of the rostrum (rounded in *P. holthuisi* s.s. vs. acute in the new species); the length of the antennular peduncles relative to the ocular peduncles (not exceeding the corneas when extended in *P. holthuisi* s.s. vs. clearly exceeding the corneas in the two new species); and the armature of the dactyls of the second and third pereopods (with dorsomesial and ventral rows of 5 spines in *P. holthuisi* s.s. vs. usually 9 or 10 in the two new species). In general appearance, the habitus of *P. holthuisi* s.s. is stouter and less armed than in the two new species, having less elongate ocular peduncles, slightly more dilated corneas, a shorter and broader right cheliped, and a nearly smooth dorsal surface on the right palm.

The color pattern described by Provenzano (1961) for the holotype from St. John, U. S. Virgin Islands, rather accurately applies to other shallow water specimens herein assigned to *P. holthuisi* s.s., especially in terms of the "carapace with symmetrically placed pairs of short longitudinal dark stripes....eyestalks with thin ring of brownish pigment on proximal third....major manus white distally....major carpus diffusely colored with purple", along with striping on the walking leg articles "imposed on a diffuse yellow background which forms a band around each segment." Unfortunately, this color description for specimens from the type locality, which was repeated by Williams (1984), has been assumed by subsequent workers to generally apply to materials assigned to this species from throughout its presumed accepted broad range. Despite some similarity in patterning, this previously reported coloration in fact bears little resemblance to striking carapace, ocular peduncle, and appendage colors seen in related species. Given this color information, most of what McLaughlin (1981b) listed from the Gulf of Mexico region as *P. holthuisi* is not likely that species, as evident from extensive subsequent collections of fresh materials from the same or nearby localities. Unfortunately, external anatomy alone does not, as yet, provide much in the way of definitive non-color characters to underpin this conclusion. The distribution stated above is conservatively limited to those specimens that can for now be assigned with reasonable confidence to *P. holthuisi* s.s., but the species likely ranges much more widely into shallow tropical waters, perhaps including those of the Bahamas, Florida Keys, southeastern Gulf of Mexico, if not more generally throughout the Caribbean and northeastern South America. Accepted records include a report from Isla Cozumel off the Caribbean coast of Quintana Roo, Mexico by Mejía-Ortíz *et al.* (2008). Provenzano (1961) considered Holthuis' (1959) report of *Pylopagurus operculatus* (Stimpson, 1859) to be synonymous with his new species, *P. holthuisi*, but concluded that Holthuis' color account of the Suriname materials appeared to differ from his own Virgin Islands type materials "...probably because of the more faded condition of the Suriname material at the time of its description." In retrospect, given the significance now placed on coloration, rereading of the Holthuis (1959) account almost certainly excludes its applying to *P. holthuisi* s.s., and instead suggests that it more closely applies to the first of two new species in the descriptions that follow (see comments for that species). At the time, Holthuis applied it to some materials he had with reservation assigned to *Pylopagurus operculatus*, which as mentioned, Provenzano (1961) later included in his synonymy for his *P. holthuisi* despite the color

differences he observed. However, it is evident that the Suriname materials came from substantially deeper waters (48–49 m) and different substrate than did the holotype from St. John (15–18 m). Recent collections of fresh material for which color establishes the identity as *P. holthuisi* s.s., all came from less than 18 m depth, with one from < 2 m, and all were taken from the immediate vicinity of coral reefs. It is uncertain as to whether larval descriptions by Gore & Scotto (1983) apply to *P. holthuisi* s.s., but the striking colors they described for postlarvae are more like those of the closely related congeners.

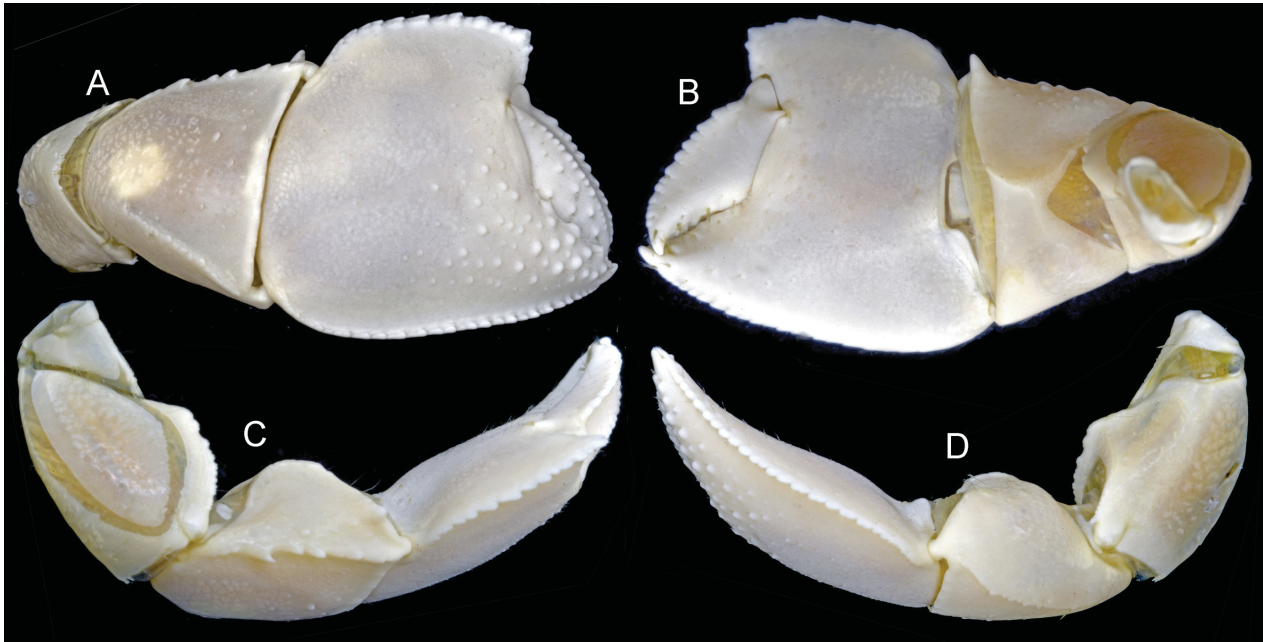


FIGURE 4. *Phimochirus holthuisi* (Provenzano, 1961) male holotype, sl 4.2 mm (USNM 105155), U. S. Virgin Islands, major cheliped. A, dorsal surface; B, ventral surface; C, mesial surface; D, lateral surface.

The precise range of *Phimochirus holthuisi* s.s. is difficult to determine with certainty, given the paucity of specimens with color information available from large portions of the western Atlantic, including from the east coast of the United States to the Caribbean and northeastern South America to Brazil. This leaves in question the precise identity of paratypes assigned by Provenzano (1961: 161), which include fragments found in fish stomachs at the U.S. Virgin Islands, and two specimens from the coast of Suriname. Based on genetic data, coloration, and the limited usefulness of morphological characters, we can herein confirm distribution of this species to include a northern range on the eastern coast of the United States off North Carolina, Central American Gulf of Mexico and Caribbean coasts from Quintana Roo and Belize, and from the Lesser Antilles in the U.S. Virgin Islands and Guadeloupe (Poupin 1986). Various reports of *P. holthuisi* from the Gulf of Mexico (Hernández-Aguilera *et al.* 1996; Rodríguez-Almaraz *et al.* 2005; Wicksten 2005), the southern Caribbean (Martínez-Campos *et al.* 2012), and Brazil (three as *Pylopagurus holthuisi*: Coelho & Ramos 1973; Coelho & Santos 1980; Coelho & Ramos-Porto 1986; and others as *Phimochirus holthuisi*: Rieger 1998; Melo 1999; Nucci & Melo 2011; Martínez-Campos *et al.* 2012; Lemaitre & Tavares 2015), all must be reevaluated to determine the extent to which they indeed may represent *P. holthuisi* s.s.

Abele & Kim's (1986) report of *Phimochirus holthuisi* is herein considered to in part represent this species as the authors used what is considered the sensu lato concept of this taxon. The report and information on *P. holthuisi* provided by Martínez-Campos *et al.* (2017) from the Caribbean coast of Colombia is, regarded to be fully consistent with *P. holthuisi* s.s. as herein defined. However, these authors reproduced McLaughlin's (1981: fig. 6) photographs of right chelipeds from three specimens whose identities remain in question, as they were originally published without additional morphological details or locality data for the photographed specimens.

***Phimochirus formani* nov. sp.**

(Figs 1; 2C, D; 5A–J; 6A–G; Tab. 1)

Pylopagurus operculatus.—Holthuis, 1959: fig. 31; Provenzano, 1961: 162 (in part); McLaughlin, 1981b: 336 (in part). [See Remarks].

Phimochirus holthuisi.—McLaughlin, 1981a: 5; McLaughlin, 1981b: 342, figs 4c, 6a–c, 7c (in part); Williams, 1984: 225 (in part), fig. 161; Rodriguez-Almaraz *et al.*, 2005: fig. 40. [See Remarks].

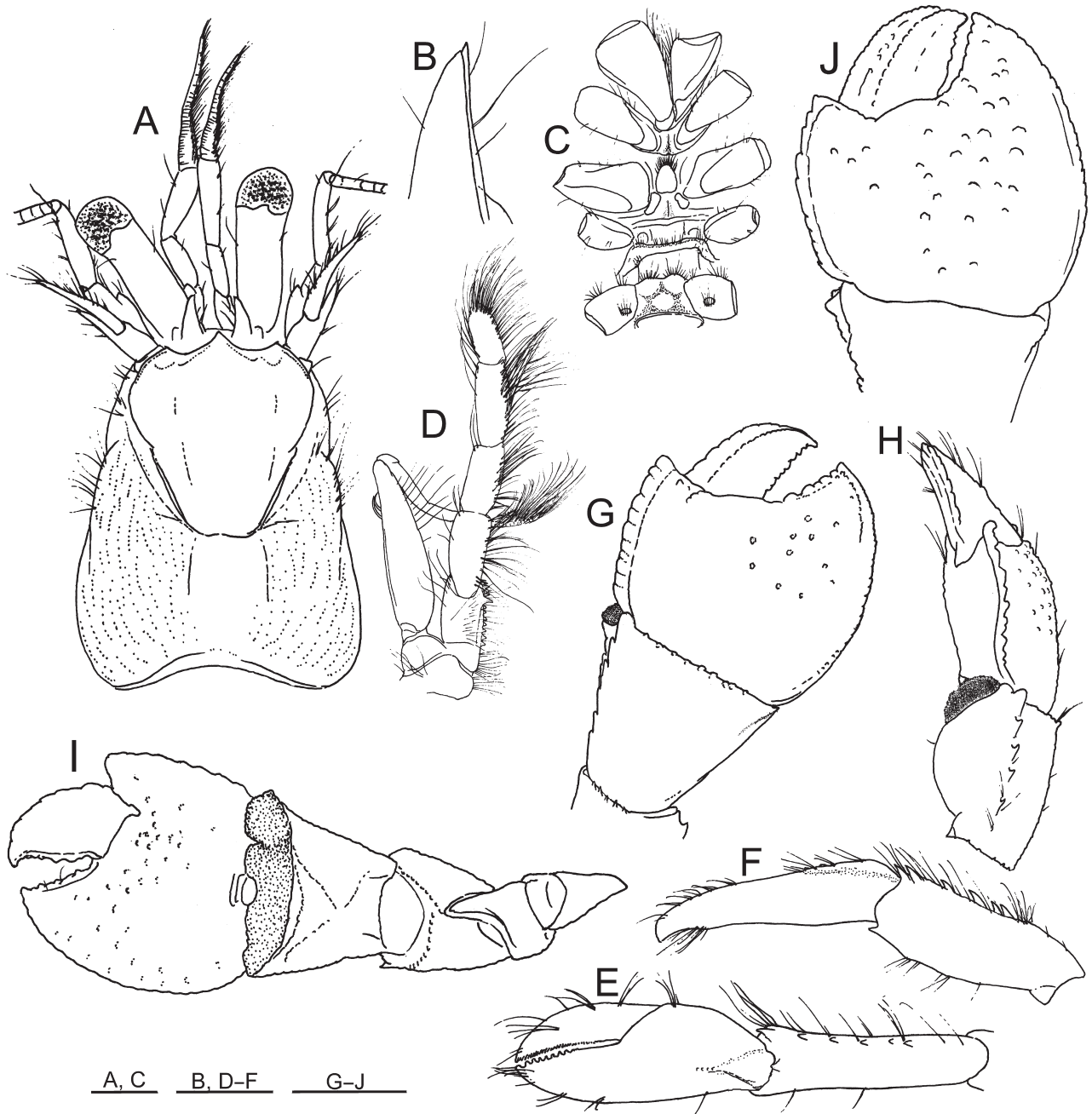


FIGURE 5. *Phimochirus formani* nov. sp. A–I, male holotype, sl 2.9 mm (USNM 1543315 = ULLZ 7841); J, male paratype, sl 3.1 mm (USNM 1547566 = ULLZ 14352); both from northeastern Gulf of Mexico. A, cephalothorax, eyes, and frontal appendages, dorsal surface; B, left ocular acicle, dorsal surface; C, thoracic sternites and coxae, ventral surface; D, right third maxilliped, external surface; E, minor (left) cheliped, dorsal surface; F, minor (left) cheliped, lateral surface; G, major (right) cheliped, dorsal surface; H, major (right) cheliped, mesial surface; I, major (right) cheliped, ventral surface; J, major (right) cheliped, dorsal surface. Scale bars = 1.0 mm (A, C–F); 0.25 mm (B); 2.0 mm (G–I).

Type material. Holotype: male, sl 2.9 mm (USNM 1543315 = ULLZ 7841), northeastern Gulf of Mexico, 28° 10.13' N, 84° 01.07' W, 42 m, northwestern Florida shelf, 5 Jul 2006.

Paratypes: *Northeastern Gulf of Mexico*. 1 male, sl 3.1 mm (USNM 1543129 = ULLZ 7685) 28° 29.64' N, 84° 27.95' W, 47 m, northwestern Florida shelf, 4 Jul 2006; 1 male, sl 2.8 mm (USNM 1543170 = ULLZ 7711) 28° 05.2' N, 83° 46.16' W, 38 m, northwestern Florida shelf, 5 Jul 2006; 1 female, sl 3.6 mm, 1 ov female, sl 4.1 mm (USNM 1543313 = ULLZ 7847) 27° 55.58' N, 83° 46.15' W, 43 m, northwestern Florida shelf, 5 Jul 2006; 1 male sl 1.6 mm, in worm tube (USNM 1543428 = ULLZ 8062) 29° 20.64' N, 85° 39.18' W, 48 m, northwestern Florida shelf, 3 July 2006; 1 female sl 6.4 mm (USNM 1543759 = ULLZ 8488) 50 m, due west of Tampa Bay, Florida, 3 Aug 1994; 1 juvenile, sl 1.2 mm, in tusk shell (USNM 1544361 = ULLZ 8950) 24° 43.37' N, 83° 13.58' W, 62 m, off Dry Tortugas, Florida, 3 Jun 2004; 1 male, sl 3.1 mm (USNM 1547566 = ULLZ 14352) 26° 12.77' N, 83° 21.18' W, 55 m, southwestern Florida shelf, 11 Jun 2012. *Northwestern Gulf of Mexico*. 1 ov female, sl 3.6 mm (USNM 1547705 = ULLZ 14572) 28° 44.76' N, 90° 14.15' W, 28 m, off Mississippi River Delta, 24 Aug 2012; 1 ov female, sl 3.4 mm (USNM 1547505 = ULLZ 14134) 29° 20.683' N, 88° 27.136' W, 63 m, off Mississippi, 23 Apr 2011. *Southeastern Gulf of Mexico*. 1 female, sl 2.4 mm, 1 ov female sl 3.3 mm (USNM 1547876 = ULLZ 14323) 24° 47.35' N, 83° 09.3' W, 56.6 m, off Florida Keys, 13 Jun 2012.

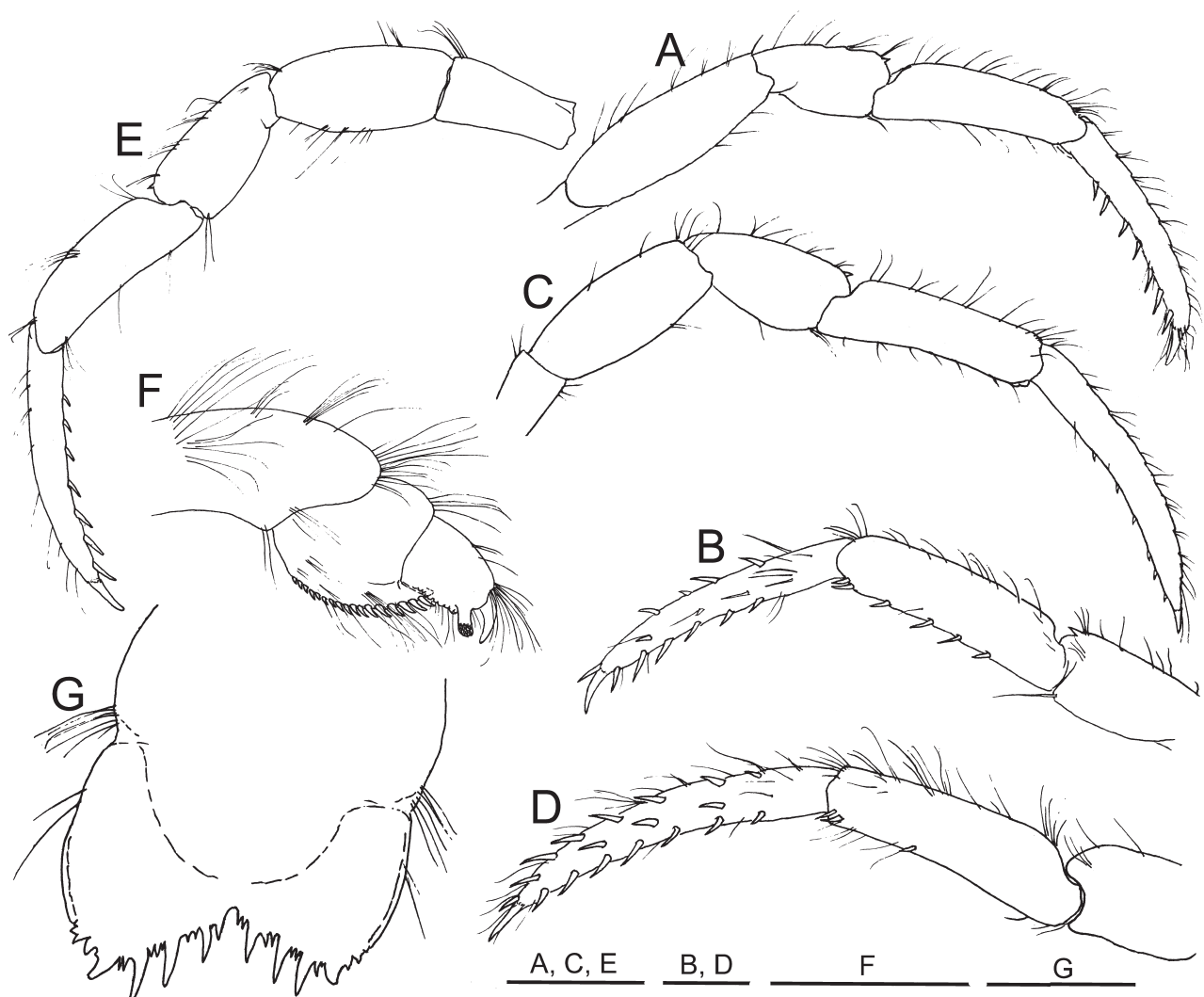


FIGURE 6. *Phimochirus formani* nov. sp. Male holotype, sl 2.9 mm (USNM 1543315 = ULLZ 7841), from northeastern Gulf of Mexico. A, right second pereopod, lateral surface; B, right second pereopod terminal articles, mesial surface; C, right third pereopod, lateral surface; D, right third pereopod terminal articles, mesial surface; E, left third pereopod, lateral surface; F, right fourth pereopod terminal articles, lateral surface; G, telson, dorsal surface. Scale bars = 2.0 mm (A, C, E); 1.0 mm (B, D, F, G).

Other material: *Northeastern Gulf of Mexico*. 1 ov female, sl 2.8 mm (USNM 103707) 29° 28' N, 85° 31' W, 21.9 m, northwestern Florida shelf, 1 Feb 1956. *Southeastern Gulf of Mexico*. 1 female, sl 1.8 mm (USNM 191095) 24° 18.5' N, 82° 20.0' W, 196–210 m, south of Marquesas Keys, 26 Apr 1969; 1 ov female, sl 3.3 mm (USNM 191096) 24° 21.5' N, 82° 26.7' W, 59–60 m, off Key West, 26 Apr 1969.

Diagnosis. Carapace shield approximately 1.1 times longer than broad; rostrum acutely triangular, reaching distally beyond lateral projections, terminating in strong spine. Antennular peduncles exceeding distal margins of cornea when fully extended by approximately one-fourth length of ultimate segment. Antennal peduncles reaching to about distal margin of corneas when fully extended, flagellum with alternating long (2 flagellar articles in length) and short setae (less than 1 flagellar article in length). Right chela with dorsal surface of fixed finger with few well-spaced low tubercles; palm smooth dorsally or with few well-spaced low tubercles distally near base of fixed finger, dorsomesial margin sinuous sharply defined as tuberculate or bluntly spinose ridge flaring distally and terminating in spine-like distal angle; carpus with dorsomesial margin sharply defined by spinose ridge including strong, mesially projecting spine. Dactyls of second and third pereopods with ventromesial row of 7–9 corneous spinules (or 4 corneous spinules in very small individuals sl < 2.0 mm). Anterior lobe of sternite between third pereopods semi-subovate, distal margin with simple setae; sternites between fourth and fifth pereopods with simple setae. GenBank sequence accession numbers for paratype (USNM 1547566 = ULLZ 14352): (H3) MK830053; (12s) MK828404; (16s) MK848222.

Description. Carapace shield (Fig. 5A) subtriangular, approximately 1.1 times longer than broad; dorsal surface glabrous except for scattered short setae medially on each side and near anterior margin, lacking linea or grooves except for weakly visible short linea and grooves separating narrow lateral lobe on each side; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping; posterior margin roundly truncate. Rostrum acutely triangular, reaching distally beyond lateral projections, terminating in strong spine. Lateral projections subtriangular, terminating in small marginal spine.

Ocular peduncles (Fig. 5A) relatively long, about 0.8 length of shield, width near even throughout; surfaces naked except tuft of short setae on mesial face medially; corneas weakly dilated. Ocular acicles (Fig. 5B) narrow (approximately 3.5 times longer than basal width), acutely subtriangular, dorsal surface concave, each terminating in small submarginal spine.

Antennular peduncles exceeding distal margins of corneas when fully extended by approximately one-fourth length of ultimate segment. Segments naked or with scattered short setae; basal segment with blunt ventromesial distal angle, and small spine on lateral face.

Antennal peduncles reaching to about distal margin of corneas when fully extended. Fifth segment slender, with few short setae on lateral and mesial margins. Fourth segment unarmed. Third segment with blunt ventrodistal angle. Second segment with dorsolateral distal angle produced into strong spine-like process with few short distolateral setae; dorsomesial distal angle with small spine. First segment unarmed laterally. Antennal acicles reaching to about proximal margin of corneas, broadly curving outward, terminating in strong spine, with few tufts of setae on mesial margin and tuft of setae distally. Flagellum long, exceeding extended right cheliped, with alternating long (2 flagellar articles in length) and short setae (less than 1 flagellar article in length).

Third maxilliped (Fig. 5D) ischium with crista dentata consisting of approximately 18–20 small, sharp teeth slightly diminishing in length distally, and accessory tooth.

Chelipeds (Fig. 5E–J) strongly dissimilar in robustness and shape, right massive and distinctly larger and stronger than left; articular membrane between chela and carpus often with fleshy protuberance (Fig. 5H, I, see Remarks). Right (major) cheliped (Fig. 5G–J) operculate, virtually naked on all surfaces except for few scattered short setae. Chela subcircular to subovate in outline; cutting edges of dactyl and fixed finger each with row of slightly unequal calcareous teeth and terminating in blunt, inwardly curved calcareous tips overlapping when closed. Dactyl slightly shorter than palm; mesial margin sharply defined, crenulate; dorsal surface with distinct median ridge, dorsomesial surface concave. Fixed finger broad basally; dorsal surface with few well-spaced low tubercles; ventrolateral margin sharply defined, crenulate. Palm smooth dorsally or with few well-spaced low tubercles distally near base of fixed finger; ventrolateral margin sharply defined, weakly crenulate (or straight in very small individuals sl < 2.0 mm); dorsomesial margin sinuous sharply defined as tuberculate or bluntly spinose ridge flaring distally and terminating in spine-like distal angle (or straight and not flaring in very small individuals < 2.0 mm); ventromesial surface smooth. Carpus approximately as long as merus; dorsal and lateral surfaces smooth, rounded, with weakly defined ridge on dorsolateral margin distally; dorsodistal margin with row of small blunt spines or tubercles; dorsomesial margin sharply defined by spinose ridge including strong, mesially projecting spine; mesial face nearly vertical, of-

ten with small distal spine; ventral surface smooth. Merus subtriangular in cross-section, surfaces smooth, unarmed except for row of small sharp spines on dorsodistal margin and spine on ventrolateral distal angle. Ischium unarmed. Coxa with row of setae on ventromesial distal angle, ventral surface with cluster of low, minute spines or tubercles proximally.

Left (minor) cheliped (Fig. 5E, F) slender, reaching to approximately mid-level of right palm, surfaces smooth, with scattered short setae; fingers terminating in inwardly curved corneous tips crossed when closed and ventrally forming spoon-like surface. Dactyl longer than palm; cutting edge with row of fused minute corneous spinules. Fixed finger broader than dactyl; cutting edge with row of minute calcareous teeth and row of fused corneous spinules. Palm dorsal surface with weak median ridge proximally, small median spine distally near cutting edges of fixed finger and dactyl. Carpus approximately as long as merus; dorsal margin with row of small sharp spines and strong dorsodistal spine; lateral surface with small ventrodistal spine. Merus subtriangular in cross-section; lateral surface with minute ventrodistal spine. Ischium and coxa unarmed, latter with row of setae on ventromesial margin.

Ambulatory pereopods 2 and 3 (Fig. 5A–E) sparsely setose, left and right subequal, each with dactyl broadly curved, approximately 1.3 times longer than propodus, terminating in sharp corneous claw curving ventrally; dorsal margins with well-spaced long setae; ventral margins with scattered short setae, with ventromesial row of 7–9 corneous spinules (or 4 corneous spinules in small individuals $sl < 2.0$ mm). Propodus nearly straight, subequal in length to carpus, with few tufts of setae dorsally, with 1 or 2 ventrodistal corneous spinules near articulation with dactyl. Carpus with small dorsodistal spine, with few setae or tufts of setae dorsally. Merus and ischium unarmed. Anterior lobe of sternite between third pereopods semisubovate (Fig. 3C), distal margin with simple setae.

Fourth pereopod (Fig. 5F) semichelate, sparsely setose. Dactyl stout, slender, terminating in inwardly curved corneous claw; dorsal margin with tuft of long setae distally; ventral margin with ventrolateral row of minute, closely-set corneous teeth, and distinctly developed brush-like preungual process at base of corneous claw. Propodal rasp with 1 row of ovate corneous scales. Carpus unarmed except for few long setae dorsally. Merus unarmed, nearly naked. Sternite between coxae rod-like, with simple setae.

Fifth pereopod chelate. Propodal rasp extending for about half length lateral surface of propodus, with long curved setae on ventrodistal angle. Sternite between coxae (Fig. 5C) with anterior lobe subdivided into 2 lobes, with distal simple setae.

Uropods markedly asymmetrical, left largest, exopods each with row of long setae dorsally; ventral margin of left and right exopods naked or with few short setae. Telson (Fig. 6G) weakly asymmetrical, longer than broad, with distinct lateral indentations; posterior lobes with corneous lateral margins, lobes separated by narrow U-shaped median cleft, terminal margins oblique, each armed with row of 4 strong, slender spines (including spine at distolateral angle) interspersed with 1 or 2 small spines.

Color. In life (Fig. 2C, D), ocular peduncle with band of deep bluish purple near midlength, broadest ventrally, dorsally disjunct, blotched with red, or partially incomplete, proximally abutted by ill-defined variable band of red; carapace shield marked by light “trident” pattern consisting of broad median whitish longitudinal bar subdivided by narrow orange center line, a similar bar to either side, lateral bars diverging from median bar anteriorly; distal margins of cheliped and anterior walking leg meri lacking lavender patches.

Etymology. The specific name was selected to honor W. Wayne Forman, a New Orleans based environmental scientist whose talents include an unusually broad grasp of marine biota, and who has over many years brokered access to research sites, acquisition of research specimens, and the securing of financial support for marine scientists working throughout the northern Gulf of Mexico.

Habitat. Occupying variety of small to medium sized gastropod shells, especially facioliariids, turbinids, and muricids; offshore calcareous banks and deep platforms around coral reefs, especially where richly covered by macroalgae and epifauna, including among rhodoliths; inner to middle continental shelf; 27–62 m.

Distribution. Western Atlantic: northeastern, northwestern, and southeastern Gulf of Mexico; Suriname.

Remarks. As previously noted under the Remarks for *Phimochirus holthuisi* s.s., McLaughlin’s (1981a, b) report of *P. holthuisi* includes three species, one of which is *P. formani* **nov. sp.** and was represented by Clade I in our molecular genetic analyses (Fig. 1). This new species, and a second new species herein described, is unmistakably distinguished in life by differences in color patterns. Aside from color differences, the two can be separated by subtle morphological differences such as the degree of armature on the dorsal surface of the right chela (with few small tubercles on the fixed finger and distal part of the palm in *P. formani* **nov. sp.** vs. numerous small tubercles on

the fixed finger and at least distal half of the palm in the other new species); relative development of the dorsomesial ridge of the right chela (sinuous and tuberculate or bluntly spinose, flaring distally in *P. formani* **nov. sp.** vs. straight, crenulate, not flaring distally in the other new species); and armature of the dactyl of the second and third pereopods (with rows of 7–9 dorsomesial and ventral corneous spinules in *P. formani* **nov. sp.** vs. rows of 10 or 11 dorsomesial and ventral corneous spinules in the other new species). However, these morphological characters must be used with caution and best in combination, as they are subject to some variations with size of specimens and thus are not absolute.

The color description that Holthuis (1959) provided for the Suriname materials that he provisionally assigned to *Pylopagurus operculatus* fits better to *Phimochirus formani* **nov. sp.** than to *P. holthuisi* s.s. Provenzano (1961) noted the color differences but, even so, included the Suriname record in the synonymy of his *Pylopagurus holthuisi* (= *Phimochirus holthuisi*). Thus, the line illustrations of Holthuis (1959: fig. 31) appear to apply to neither *Pylopagurus operculatus* (= *Phimochirus operculatus*), as originally reported, nor to *Phimochirus holthuisi* s.s., but instead most likely to *P. formani* **nov. sp.** A fleshy protrusion of the joint membrane between the major cheliped carpus and propodus, somewhat similar to that reported in *P. operculatus*, is evident in some specimens. While *P. formani* **nov. sp.** occurs sympatrically with the other herein described new species, in regional collections to date the former appears to be more common than the latter in the eastern Gulf of Mexico, while the other new species is more common in samples from the western Gulf.

The illustration published by Holthuis (1959, fig. 31) for *Pylopagurus operculatus*, subsequently discussed by Provenzano (1961), was reproduced in whole or in part by Williams (1984) and Rodríguez-Almaraz *et al.* (2005) and is herein considered to represent *Phimochirus formani* **nov. sp.**

***Phimochirus tunnelli* nov. sp.**

(Figs 1; 2E, F; 7 A–J; 8A–H; Tab. 1)

Phimochirus holthuisi.—McLaughlin, 1981a: 5; McLaughlin, 1981b: 342, figs 4c, 6a–c, 7c (in part; see Remarks under *P. holthuisi* s.s. and *P. formani* **nov. sp.**)

Phimochirus sp.—Felder *et al.*, 2014: 813, fig. 7b.

Type material. Holotype: male sl 6.3 mm (USNM 1547302 = ULLZ 13837) northwestern Gulf of Mexico, 28° 05.684' N, 91° 05.22' W, 55 m, Louisiana shelf bank, 29 Aug 2011.

Paratypes: *Northeastern Gulf of Mexico*. 1 juvenile male, sl 1.9 mm (USNM 1543319 = ULLZ 7973) 28° 50.74' N, 85° 02.11' W, 52 m, northwestern Florida shelf; 1 female, sl 3.1 mm (USNM 1543432 = ULLZ 8164) 29° 43.32' N, 85° 54.84' W, 38 m, northwestern Florida shelf, 2 Jul 2006. *Northwestern Gulf of Mexico*. 2 males, sl 3.0, 4.7 mm, 1 ov female, sl 3.9 mm (USNM 1541146 = ULLZ 5789) 28° 06.3' N, 29° 01.6' W, 66 m, Ewing Bank, Louisiana shelf, 1 Aug 2002; 2 males, sl 2.5, 3.3 mm, 1 ov female, sl 3.9 mm (USNM 1543233 = ULLZ 7825) 27° 56.46' N, 92° 00.03' W, 70 m, off Louisiana, 9 Jul 2006; 1 male, sl 4.1 mm (USNM 1545269 = ULLZ 10611) 27° 59.141' N, 91° 38.382' W, 68 m, Louisiana shelf deep bank, 1 Jul 2001; 1 male, sl 4.4 mm, (USNM 1558304 = ULLZ 17898) 27° 54.961' N, 92° 23.01' W, 80 m, Louisiana shelf bank, 9 May 2018; 1 female, sl 2.1 mm (USNM 1558291 = ULLZ 17909) 27° 58.925' N, 91° 39.779' W, 72 m, Louisiana shelf bank, 6 May 2018. *Southwestern Gulf of Mexico*. 1 male, sl 2.8 mm (USNM 1544265 = ULLZ 9359) 22° 16.08' N, 90° 42.89' W, 55 m, western Campeche shelf, Mexico, 18 Jun 2005; 1 juvenile male, sl 2.1 mm (USNM 1541878 = ULLZ 7021) 22° 07.98' N, 91° 23.75' W, 49 m, western Campeche shelf, Mexico, 17 Jun 2005; 1 ov female, sl 3.2 mm (USNM 1544260 = ULLZ 9354) 21° 06.64' N, 92° 08.72' W, 47 m, western Campeche shelf, Mexico, 9 Jun 2005. *Southeastern Gulf of Mexico*. 1 ov female sl 5.7 mm, (USNM 1541669 = ULLZ 5814) 24° 38.27' N, 83° 36.36' W, 65 m, off Dry Tortugas, Florida, 3 Jun 2004; 1 male, sl 3.7 mm (USNM 1544363 = ULLZ 8954) 24° 41.73' N, 83° 36.48' W, 64 m, off Florida Keys, 1 Jun 2004.

Other material. *Northeastern Gulf of Mexico*. 3 females (1 ov), sl 3.4–3.7 mm (USNM 1549242 = ULLZ 16182) 25° 03.354' N, 83° 43.559' W, 83 m, southwestern Florida shelf, 9 Sep 2014; 1 male, sl 2.8 mm (USNM 1549449 = ULLZ 16244) 24° 48.929' N, 83° 40.609' W, 66 m, off Florida Keys, 10 Sep 2014; 1 male, sl 5.1 mm (USNM 1549196 = ULLZ 16088) 24° 45.723' N, 83° 35.305' W, 67 m, off Florida Keys, 10 Sep 2014; 1 male, sl 3.6 mm (USNM 103706) 29° 28' N, 85° 31' W, 21.9 m, northwestern Florida shelf, 1 Feb 1956; 2 males, sl 4.8, 6.6 mm (USNM 1253344) 25° 16'54" N, 83° 37'48" W, 73 m, southwestern Florida shelf, 5 Mar 1984. *Northwestern Gulf of Mexico*. 2 males, sl 4.0, 4.5 mm (USNM 1549372 = ULLZ 16123) 28° 05.542' N, 91° 01.697' W, 58 m, off

Louisiana, 14 Sep 2014; 1 male, sl 6.0 mm, 3 females, sl 2.1–3.9 mm (USNM 1549147 = ULLZ 16113) 28° 05.382' N, 91° 06.742' W, 58 m, off Louisiana, 14 Sep 2014; 1 ov female, sl 4.6 mm (USNM 1549102 = ULLZ 16106) 28° 05.542' N, 91° 01.697' W, 58 m, off Louisiana, 14 Sep 2014; 1 male, sl 5.2 mm (USNM 1548210 = ULLZ 15181) 28° 05.552' N, 91° 01.825' W, 57 m, Ewing Bank, off Louisiana, 19 Oct 2013.

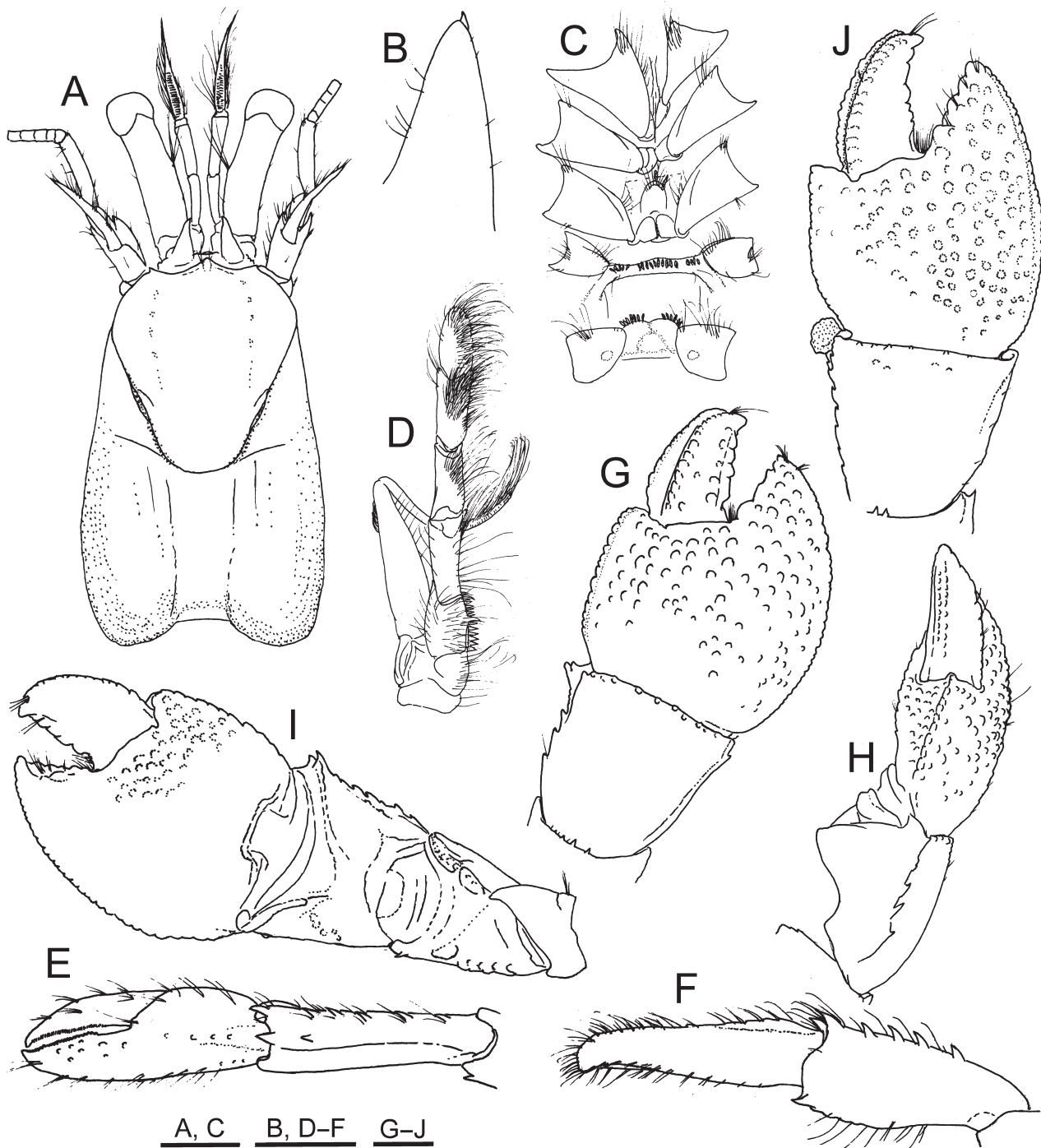


FIGURE 7. *Phimochirus tunnelli* nov. sp. A–I, male holotype, sl 6.3 mm (USNM 1547302 = ULLZ 13837), northwestern Gulf of Mexico; J, ovigerous female paratype, sl 5.7 mm (USNM 1541669 = ULLZ 5814), southeastern Gulf of Mexico. A, cephalothorax, eyes, and frontal appendages, dorsal surface; B, left ocular acicle, dorsal surface; C, thoracic sternites and coxae, ventral surface; D, right third maxilliped, external surface; E, minor (left) cheliped, dorsal surface; F, minor (left) cheliped, lateral surface; G, major (right) cheliped, dorsal surface; H, major (right) cheliped, mesial surface; I, major (right) cheliped, ventral surface; J, major (right) cheliped, dorsal surface. Scale bars = 2.0 (A, C–J); 0.5 (B).

Diagnosis. Carapace shield approximately 1.1 times longer than broad; rostrum acutely triangular, reaching distally beyond lateral projections, terminating in strong spine. Antennular peduncles reaching to distal margins of corneas when fully extended. Antennal peduncles reaching to approximately midlevel of corneas when fully extended; flagellum with short setae 1 to < 1 flagellar articles in length. Right chela with dorsal surface of fixed finger covered with well-spaced low tubercles; palm with numerous well-spaced tubercles or blunt spines on distal half, dorsomesial margin sharply defined as straight (in mesial view) crenulate or bluntly spinulose ridge terminating in rounded or spine-like angle; carpus with dorsomesial margin sharply defined by ridge with 3 or 4 sharp proximal spines and 2 or 3 smaller blunt distal spines. Dactyls of second and third pereopods with 3 rows of corneous spinules, one dorsomesial with 10 or 11, one ventromesial with 5–10, and one ventral with 9–11. Anterior lobe of sternite between third pereopods semisubovate, distal margin with simple and often capsulate setae; sternites between fourth and fifth pereopods with simple setae and often short capsulate setae. GenBank sequence accession numbers for holotype (USNM 1547302 = ULLZ 13837): (12s) MK848209; (16s) MK848226.

Description. Carapace shield (Fig. 7A) subtriangular, approximately 1.1 times longer than broad; dorsal surface glabrous except for scattered short setae medially on each side and near anterior margin, lacking lineae or grooves except for weakly visible short lineae and grooves separating narrow lateral lobe on each side; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping; posterior margin roundly truncate. Rostrum acutely triangular, reaching distally beyond tip of lateral projections, terminating in spine. Lateral projections subtriangular, terminating bluntly or in small marginal spine.

Ocular peduncles (Fig. 7A) relatively long, about 0.7 length of shield, width near equal throughout; surfaces naked except tuft of short setae medially on mesial and lateral faces; corneas weakly dilated. Ocular acicles (Fig. 7B) narrow (approximately 2.3 times longer than basal width), acutely subtriangular, with dorsal surface concave, each terminating in small submarginal spine.

Antennular peduncles reaching to distal margins of corneas when fully extended. Segments naked or with scattered short setae; basal segment with blunt ventromesial distal angle, and small spine on lateral face.

Antennal peduncles reaching to approximately midlevel of corneas when fully extended. Fifth segment slender, with few short setae on lateral and mesial margins. Fourth segment unarmed. Third segment with small spine on ventrodistal angle. Second segment with dorsolateral distal angle produced into strong spine-like process with few short distolateral setae; dorsomesial distal angle with small spine. First segment unarmed laterally. Antennal acicles not reaching proximal margin of corneas, broadly curving outward, terminating in strong spine, with few tufts of setae on mesial margin and tuft of setae distally. Flagellum long, exceeding extended right cheliped, with short setae 1 to < 1 flagellar articles in length.

Third maxilliped (Fig. 7D) ischium with crista dentata consisting of approximately 18–20 small, sharp teeth slightly diminishing in length distally, and accessory tooth.

Chelipeds (Fig. 7E–J) strongly dissimilar in robustness and shape, right massive and distinctly larger and stronger than left; articular membrane between chela and carpus often with fleshy protuberance (see Remarks under *P. formani* **nov. sp.**). Right (major) cheliped (Fig. 7G–J) operculate, virtually naked on all surfaces except for few scattered short setae. Chela subcircular in outline; cutting edges of dactyl and fixed finger each with row of slightly unequal calcareous teeth and terminating in blunt, inwardly curved calcareous tips overlapping when closed. Dactyl slightly shorter than palm; mesial margin sharply defined by bluntly spinulose ridge; dorsal surface with distinct median ridge, dorsomesial surface concave. Fixed finger broad basally; dorsal surface with few well-spaced low tubercles or blunt spines; lateral margin sharply defined by bluntly spinulose ridge. Palm with numerous well-spaced tubercles or blunt spines on distal half; ventrolateral margin sharply defined by weakly spinose ridge; dorsomesial margin sharply defined as straight crenulate or bluntly spinulose ridge terminating in rounded or spine-like angle; ventromesial surface smooth. Carpus approximately as long or slightly shorter than merus; dorsal and lateral surfaces smooth, rounded, with weakly defined ridge on dorsolateral margin distally; dorsodistal margin with row of minute tubercles; dorsomesial margin sharply defined by ridge of 3 or 4 sharp proximal spines and 2 or 3 smaller blunt distal spines; mesial surface nearly vertical, distal portion somewhat flaring and armed with 3 small spines; ventral surface smooth. Merus subtriangular in cross-section, surfaces smooth, unarmed except for row sharp spines on dorsodistal margin and spine on ventrolateral distal angle. Ischium unarmed. Coxa with ventrolateral margin bluntly spinulose, row of setae on ventromesial distal angle.

Left (minor) cheliped (Fig. 7E, F) slender, reaching to approximately mid-level of right palm, surfaces smooth, with scattered short setae; fingers terminating in inwardly curved corneous tips crossed when closed and ventrally

forming spoon-like surface. Dactyl slightly longer than palm; cutting edge with row of fused minute corneous spinules. Fixed finger broader than dactyl; cutting edge with row of minute calcareous teeth and row of fused corneous spinules; dorsal surface smooth or with scattered small low tubercles. Palm dorsal surface with weak median minutely spinulose ridge proximally, and small median spine distally near cutting edges of fixed finger and dactyl. Carpus approximately as long as merus; dorsomesial margin with row of 5 spines, dorsolateral margin with 2 spines distally; lateral surface with small ventrodistal spine. Merus subtriangular in cross-section; lateral surface with small ventrodistal spine. Ischium and coxa unarmed, latter with row of setae on ventromesial margin.

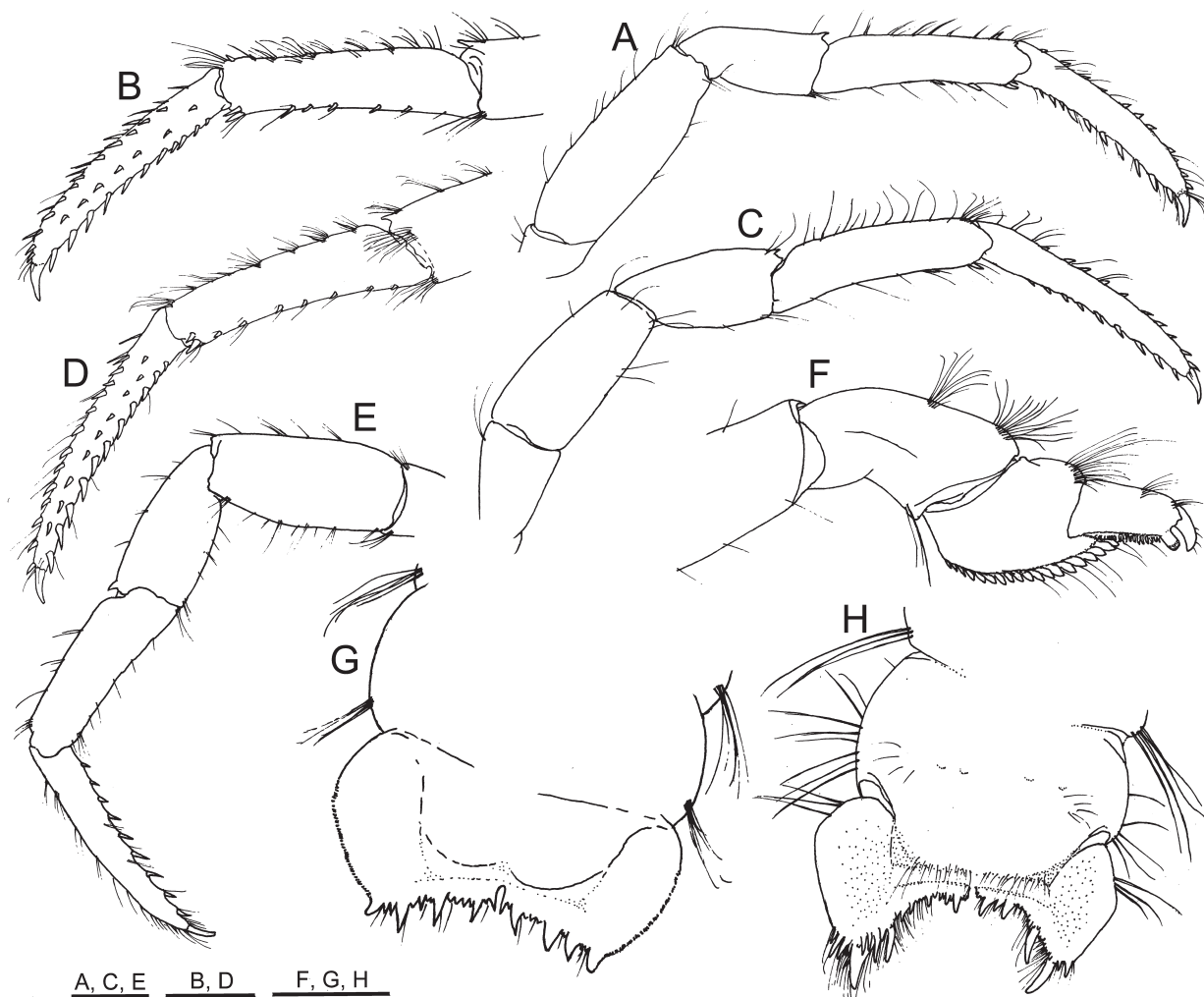


FIGURE 8. *Phimochirus tunnelli* nov. sp. A–G, male holotype, sl 6.3 mm (USNM 1547302 = ULLZ 13837), northwestern Gulf of Mexico; H, ov female paratype, sl 5.7 mm (USNM 1541669 = ULLZ 5814), southeastern Gulf of Mexico. A, right second pereopod, lateral surface; B, right second pereopod terminal articles, mesial surface; C, right third pereopod, lateral surface; D, right third pereopod terminal articles, mesial surface; E, left third pereopod, lateral surface; F, right fourth pereopod terminal articles, lateral surface; G, H, telson, dorsal surface. Scale bars = 2.0 mm (A–E); 1.0 mm (F, H); 1.5 mm (G).

Ambulatory pereopod 2 and 3 sparsely setose (Fig. 8A–E), left and right subequal. Each with dactyl broadly curved, approximately 1.3 times longer than propodus, terminating in sharp corneous claw curving ventrally; dorsal margins with well-spaced long setae; with 3 rows of corneous spinules, one dorsomesial with 10 or 11, one ventromesial with 5–10, and one ventral with 9–11. Propodus nearly straight, subequal in length to carpus, with few tufts of setae dorsally; ventral margin with row of 4 corneous spinules in addition to 2 corneous spinules near articulation with dactyl. Carpus with small dorsodistal spine, with few setae or tufts of setae dorsally. Merus and ischium unarmed. Anterior lobe of sternite between third pereopods semisubovate (Fig. 7C), distal margin often with capsulate, in addition to simple, setae.

Pereopod 4 (Fig. 8F) semichelate, sparsely setose. Dactyl stout, slender, terminating in inwardly curved corneous claw; dorsal margin with tuft of long setae distally; ventral margin with ventrolateral row of minute, closely-set

corneous teeth, and distinctly developed brush-like preungual process at base of corneous claw. Propodal rasp with 1 row of ovate corneous scales. Carpus unarmed except for few long setae dorsally. Merus unarmed, nearly naked. Sternite between coxae (Fig. 7C) rod-like, with simple setae and often short capsulate setae.

Pereopod 5 chelate. Propodal rasp extending for about half length lateral surface of propodus, with long curved setae on ventrodiscal angle. Anterior lobe of sternite between coxae subdivided (Fig. 7C), with simple setae and often capsulate setae distally.

Uropods markedly asymmetrical, left largest, exopods each with row of long setae dorsally; ventral margin of left and right exopods with long setae distally. Telson (Fig. 8G, H) weakly asymmetrical, longer than broad, with distinct lateral indentations; posterior lobes with corneous lateral margins, lobes separated by narrow U-shaped median cleft, terminal margins oblique, each armed with row of 4 strong, slender spines (including spine at distolateral angle) interspersed with 1 or 2 small spines.

Color. In life (Fig. 2E, F), ocular peduncle with usually complete band of lavender near midlength, abutted by narrower band of dark orange proximally; carapace shield lacking light “trident” pattern, near uniformly orange or marked by large spot or subquadrate area of dark orange anteriorly; distal margins of cheliped and anterior walking leg meri marked by lavender patches.

Etymology. The specific name is assigned in recognition of the late John W. (Wes) Tunnell, formerly of Texas A&M University–Corpus Christi, whose deep appreciation for, and professional understanding of, coastal and marine biodiversity in the Gulf of Mexico region is reflected in many books and other publications that he authored or orchestrated over his long and productive career.

Habitat. Occupying varied medium sized gastropod shells, especially faciolariids, turbinids, and muricids; offshore rhodolith and other calcareous banks, especially where richly covered by macroalgae and epifaunal communities; inner to middle continental shelf; 38–72 m.

Distribution. Western Atlantic: northeastern, northwestern, and southeastern Gulf of Mexico.

Remarks. *Phimochirus tunnelli* **nov. sp.**, corresponding to Clade II in our molecular genetic analyses (Fig. 1), was long confused under the name *P. holthuisi*, as was *P. formani* **nov. sp.** Available collections of *P. tunnelli* suggest this species averages slightly larger sizes than does *P. formani* **nov. sp.**, but both species can exceed 6.0 mm in shield length, somewhat larger than any known specimen of *P. holthuisi* s.s. *P. tunnelli* **nov. sp.** is among the most common of benthic decapods on deep banks of the northern Gulf of Mexico, especially on rhodolith-covered calcareous banks of the northwestern Gulf. Following marked declines in other benthic decapod species on such banks after the Deepwater Horizon oil spill, populations of this new species recovered to dominate decapod abundances in those habitats (Felder *et al.* 2014: fig. 7b).

A noteworthy setal type and some morphological variations were observed in *Phimochirus tunnelli* **nov. sp.** The sternites between the third to fifth pereopods frequently bear tear-shaped capsulate setae, though these are more frequently seen in males than in females. The anterior lobe of the sternite between the third pereopods is semisubovate but in larger specimens such as in an ovigerous female (sl 5.7 mm, USNM 1541669 = ULLZ 5814), it is noticeably narrow and more elongated. In that same ovigerous female, the armature of the terminal margins of the posterior lobes of the telson (Fig. 8G, H) is visibly stronger, with more numerous interspersed spines in between the larger ones than in other specimens, and with the anterolateral angles each having a strong, curved terminal spine and 2 additional spines laterally.

Acknowledgements

For assisting with access to comparative materials for this study, we thank K. Reed, S. Pecnik, and other support staff of the Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., along with A. Bemis and G. Paulay, Florida Natural History Museum, University of Florida, Gainesville. Among many colleagues who assisted with field sampling, logistics, and analyses for this project, we thank F. Álvarez, H. Bracken-Grissom, R. Collin, E. Escobar, J. Felder, S. Fredericq, E. Garcia, S. Jones, F. Mantelatto, E. Palacios-Theil, V. Paul, S. Pecnik, S. Rabalais, R. Robles, W. Schmidt, B. Thoma, and A. Windsor. Work was supported by funding to DLF from the U.S. National Science Foundation grants NSF/BS&I DEB-0315995, NSF/AToL EF-0531603, and NSF.RAPID DEB 1045690, along with U.S. Department of Energy grant no. DE-FG02-97ER1220. This is UL Lafayette Laboratory for Crustacean Research contribution number 193 and Smithsonian Caribbean Coral Reef Ecosystems Program contribution number 1026.

References

- Abele, L.G. & Kim, W. (1986) An illustrated guide of the marine decapod crustaceans of Florida. *State of Florida Department of Environmental Regulation*, Technical Series, 8 (1), Parts 1, 2, 1–760.
- Buhay, J.E., Moni G., Mann, N. & Crandall, K.A. (2007) Molecular taxonomy in the dark: evolutionary history, phylogeography, and diversity of cave crayfish in the subgenus *Aviticambarus*, genus *Cambarus*. *Molecular Phylogenetics and Evolution*, 42, 435–448.
<https://doi.org/10.1016/j.ympev.2006.07.014>
- Castresana, J. (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*, 17, 540–552.
<https://doi.org/10.1093/oxfordjournals.molbev.a026334>
- Crandall, K.A. & Fitzpatrick, Jr. J.F. (1996) Crayfish molecular systematics: using a combination of procedures to estimate phylogeny. *Systematic Biology*, 45, 1–26.
<https://doi.org/10.1093/sysbio/45.1.1>
- Coelho, P.A. & Ramos, M. de A. (1973) A constituição e a distribuição da fauna de decápodos do litoral leste da América do Sul entre as latitudes 5° N e 39° S. *Trabalhos Oceanográficos da Universidade Federal de Pernambuco, Recife*, 13, 133–236. [1972]
<https://doi.org/10.5914/tropocean.v13i1.2555>
- Coelho, P.A. & Ramos-Porto, M. (1986) Sinopse dos crustáceos decápodos brasileiros (famílias Callianassidae, Callianideidae, Upogebiidae, Parapaguridae, Paguridae, Diogenidae). *Trabalhos Oceanográficos da Universidade Federal de Pernambuco, Recife*, 19, 27–53. [1985]
<https://doi.org/10.5914/tropocean.v19i1.2615>
- Coelho, P.A. & Santos, M.F.B.A. (1980) Zoogeografia marinha do Brasil. I. Considerações gerais sobre o método e aplicação a um grupo de crustáceos (Paguros: Crustácea Decápoda, super-famílias Paguroidea e Coenobitoidea). *Boletim do Instituto Oceanográfico, São Paulo*, 29 (2), 139–144.
<https://doi.org/10.1590/S0373-55241980000200029>
- Coelho, P.A., Almeida, A.O. de, Bezerra, L.E.A. & Soza, J.F.de-Filho. (2007) An updated checklist of decapod crustaceans (infraorderes Astacidea, Thalassinidea, Polychelida, and Anomura) from northern and northeastern Brazilian coast. *Zootaxa*, 1519 (1), 1–16.
<https://doi.org/10.11646/zootaxa.1519.1.1>
- Colgan, D.J., McLauchlan, A., Wilson, G.D.F., Livingston, S.P., Edgecombe, G.D., Macaranas, J., Cassis, G. & Gray, M.R. (1998) Histone H3 and U2 snRNA DNA sequences and arthropod molecular evolution. *Australian Journal of Zoology*, 46, 419–437. <https://doi.org/10.1071/ZO98048>
- Felder, D.L. (1973) An annotated key to crabs and lobsters (Decapoda, Reptantia) from coastal waters of the northwestern Gulf of Mexico. *Publications of the Center for Wetland Resources*, LSU-SG-73-02, 1–103, figs. 1–179.
- Felder, D.L., Álvarez, F., Goy, J.W. & Lemaitre, R. (2009) Decapoda (Crustacea) of the Gulf of Mexico, with comments on the Amphionidacea. In: Felder, D.L. & Camp, D.K. (Eds.), *Gulf of Mexico Origin, Waters, and Biota. Vol. 1. Biodiversity*. Texas A&M University Press, College Station, pp. 1019–1104.
- Felder, D.L., Thoma, B.P., Schmidt, W.E., Sauvage, T., Self-Krayesky, S.L., Chistoserdov, A., Bracken-Grissom, H.D. & Fred-ericq, S. (2014) Seaweeds and Decapod Crustaceans on Gulf Deep Banks after the Macondo Oil Spill. *BioScience*, 64, 808–819. <https://doi.org/10.1093/biosci/biu119>
- Forest, J., de Saint Laurent, M., McLaughlin, P.A. & Lemaitre, R. (2000) The marine fauna of New Zealand: Paguridea (Decapoda: Anomura) exclusive of the Lithodidae. *NIWA Biodiversity Memoir*, 114, 1–250.
- Gore, R.H. & Scotto, L.E. (1983) Studies on decapod Crustacea from the Indian River region of Florida, 27. *Phimochirus holthuisi* (Provenzano, 1961) (Anomura: Paguridae): the complete larval development under laboratory conditions, and the systematic relationships of its larvae. *Journal of Crustacean Biology*, 3 (1), 93–116.
<https://doi.org/10.2307/1547856>
- Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41, 95–98. https://doi.org/10.14601/Phytopathol_Mediterr-14998u1.29
- Hazlett, B.A. (1966) Social behavior of the Paguridae and Diogenidae of Curaçao. *Studies on the Fauna of Curaçao and other Caribbean Islands*, 23 (88), 1–142.
- Hernández Aguilera, J.L., Toral Almazán, R.E. & Ruiz Nuño, J.A. (1996) *Especies catalogadas de crustáceos estomatópodos y decápodos para el Golfo de México, Rio Bravo, Tamps. a Progreso, Yuc.* Dirección General de Oceanografía Naval, Secretaría de Marina y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Tampico, Tamaulipas, 132 pp.
- Holthuis, L.B. (1959) The Crustacea Decapoda of Suriname (Dutch Guiana). *Zoologische Verhandelingen*, 44 (1), 1–296.
- Katoh, K., Rozewicki, J. & Yamada, K.D. (2017) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics*, 2017, bbx108.
<https://doi.org/10.1093/bib/bbx108>
- Lemaitre, R. & McLaughlin, P.A. (2003) Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with descriptions of new genera and species. Addendum and taxonomic summary. *Proceedings of the Biological Society of Washington*, 116 (2), 464–486.

- Lemaitre, R. & Tavares, M. (2015) New taxonomic and distributional information on hermit crabs (Crustacea: Anomura: Paguroidea) from the Gulf of Mexico, Caribbean Sea, and Atlantic coast of South America. *Zootaxa*, 3994 (4), 451–506. <https://doi.org/10.11646/zootaxa.3994.4.1>
- Maddison, W.P. & Maddison, D.R. (2017) Mesquite: a modular system for evolutionary analysis. Version 3.2. Available from: <http://mesquiteproject.org> (accessed 20 August 2019)
- Martínez-Campos, B., Campos, N.H. & Bermúdez Tobón, A. (2012) Distribución de cangrejos ermitaños (Anomura: Paguroidea) en el mar Caribe colombiano. *Revista de Biología Tropical*, 60 (1), 233–252. <https://doi.org/10.15517/rbt.v60i1.2758>
- Martínez-Campos, B., Campos, N.H. & Lemaitre, R. (2017) *Catálogo de los cangrejos ermitaños del Caribe colombiano / Catalog of hermit crabs from Colombian Caribbean*. Instituto de Investigaciones Marinas y Costeras-INVEMAR Serie de Publicaciones Especiales del INVEMAR # 32. Instituto de Investigaciones Marinas y Costeras-INVEMAR, Santa Marta, Colombia, 440 pp.
- McLaughlin, P.A. (1981a) Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species: Part 1. Ten new genera of the Paguridae and a redescription of *Tomopagurus* A. Milne Edwards and Bouvier. *Bulletin of Marine Science*, 31 (1), 1–30.
- McLaughlin, P.A. (1981b) Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species: Part 2. *Rhodochirus* McLaughlin and *Phimochirus* McLaughlin. *Bulletin of Marine Science*, 31 (2), 329–365.
- McLaughlin, P.A. (2003) Illustrated keys to families and genera of the superfamily Paguroidea (Crustacea: Decapoda: Anomura), with diagnoses of genera of Paguridae. *Memoirs of Museum Victoria*, 60, 111–144. <https://doi.org/10.24199/j.mmv.2003.60.16>
- McLaughlin, P.A., Komai, T., Lemaitre, R. & Rahayu, D.L. (2010) Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostylidae and Galatheidae of the Galatheoidea). Part 1, Lithodoidea, Lomisoidea and Paguroidea. *The Raffles Bulletin of Zoology*, 23 (Supplement), 5–107.
- Mejía-Ortiz, L.M., López-Mejía, M. & Muñoz-Gómez, A.V. (2008) Crustáceos Decápodos. (Chapter 13). In: Mejía-Ortiz, L.M. (Ed.), *Biodiversidad Acuática de la Isla de Cozumel*. Universidad de Quintana Roo, Plaza y Valdés, México, pp. 225–238.
- Melo, G.A.S. (1999) *Manual de Identificação dos Crustacea Decapoda do litoral brasileiro: Anomura, Thalassinidea, Palinuridea, Astacidea*. Editora Plêiade, São Paulo, 551 pp.
- Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, Louisiana, 2010, 1–8. <https://doi.org/10.1109/GCE.2010.5676129>
- Nucci, P.R. & Melo, G.A.S. de (2011) Hermit crabs from Brazil: Family Paguridae (Crustacea: Decapoda: Paguroidea), except *Pagurus*. *Zootaxa*, 3104 (2), 26–41. <https://doi.org/10.11646/zootaxa.3104.1.2>
- Palumbi, S., Martin, A., Romano, S., McMillan, W.O., Stice, L. & Grabowski, G. (1991) *The Simple Fool's Guide to PCR*. Department of Zoology and Kewalo Marine Laboratory, Honolulu, 43 pp.
- Provenzano, A.J. Jr. (1961) Pagurid crabs (Decapoda Anomura) from St. John, Virgin Islands, with descriptions of three new species. *Crustaceana*, 3 (2), 151–166. <https://doi.org/10.1163/156854061X00644>
- Poupin, J. (2018) *Les Crustacés décapodes des Petites Antilles. Avec des nouvelles observations pour Saint-Martin, la Guadeloupe et la Martinique*. Muséum national d'Histoire naturelle, Paris, 264 pp.
- Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, 67, 901–904. <https://doi.org/10.1093/sysbio/syy032>
- Rieger, P.J. (1998) Malacostraca—Eucarida. Paguroidea. In: Young, P.S. (Ed.), *Catalogue of Crustacea of Brazil*. Museu Nacional, Rio de Janeiro, pp. 413–429. [Série Livros No. 6]
- Rodríguez, G. (1980) *Los crustáceos decápodos de Venezuela*. Instituto Venezolano de Investigaciones Científicas, Caracas, 494 pp.
- Rodríguez-Almaraz, G.A. & Zavala-Flores, J.C. (2005) 9. Cangrejos ermitaños. In: Hernández-Aguilera, J.L., Ruiz-Nuño, J.A., Toral-Almazán, R.E. & Arenas-Fuentes, V. (Eds.), *Camarones, Langostas y Cangrejos de la Costa Este de México*. Vol. 1. Comisión para el Conocimiento y Uso de la Biodiversidad (Conabio), México, pp. 263–335.
- Rodríguez, F.J., Oliver, J.L., Marín, A. & Medina, J.R. (1990) The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology*, 142, 485–501. [https://doi.org/10.1016/S0022-5193\(05\)80104-3](https://doi.org/10.1016/S0022-5193(05)80104-3)
- Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Sánchez, M.H. (1978) *Pylopagurus samariensis* sp. nov. (Crustacea, Anomura, Paguridae) de la costa del Caribe colombiano. *Anales del Instituto de Investigaciones Marinas de Punta de Betín*, 9, 215–223. [1977]

<https://doi.org/10.25268/bimc.invemar.1977.9.0.528>

- Sánchez, M.H. & Campos, N.H. (1978) Los cangrejos ermitaños (Crustacea, Anomura, Paguridae) de la costa norte colombiana. *Anales del Instituto de Investigaciones Marinas de Punta de Betín*, 10, 15–62.
<https://doi.org/10.25268/bimc.invemar.1978.10.0.503>
- Schubart, C.D., Cuesta, J.A. & Felder, D.L. (2002) Glyptograpsidae, a new brachyuran family from Central America: larval and adult morphology, and a molecular phylogeny of the Grapsoidea. *Journal of Crustacean Biology*, 22, 28–44.
<https://doi.org/10.1163/20021975-99990206>
- Stamatakis, A. (2006) RAxML–VI–HPC: maximum likelihood–based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
<https://doi.org/10.1093/bioinformatics/btl446>
- Thoma, B.P., Guinot, D. & Felder, D.L. (2014) Evolutionary relationships among American mud crabs (Crustacea: Decapoda: Brachyura: Xanthoidea) inferred from nuclear and mitochondrial markers, with comments on adult morphology. *Zoological Journal of the Linnean Society*, 70, 86–109.
<https://doi.org/10.1111/zoj.12093>
- Tudge, C.C., Asakura, A. & Ahyong, S.T. (2012) Infraorder Anomura MacLeay, 1838. In: Schram, F.R. & Von Vaupel Klein, J.C. (Eds.), *Treatise on Zoology – Anatomy, Taxonomy, Biology. Crustacea*, 9B (70), 221–333.
https://doi.org/10.1163/9789047430179_005
- Wicksten, M.K. (2005) Decapod crustaceans of the Flower Garden Banks National Marine Sanctuary. *Gulf of Mexico Science*, 23 (1), 30–37.
<https://doi.org/10.18785/goms.2301.04>
- Williams, A.B. (1984) *Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida*. Smithsonian Institution Press, Washington, D.C., 550 pp.